

The eastern boundary of the geographic range of the Pallas' spadefoot *Pelobates vespertinus* (Anura, Amphibia) is limited by overwintering temperatures

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Abstract

We studied the relationship between the geographic distribution of the Pallas' spadefoot (*Pelobates vespertinus*) and the soil temperature regime at the eastern boundary of this species' range (south-western West Siberia and northwest Kazakhstan). This species overwinters underground, burrowing down to 1.5 m or deeper and has poor frost tolerance – it is unable to withstand temperatures below 0 °C, therefore, the temperature at its overwintering depth has to be above zero. A cartographic approach to identifying the distribution of zero isotherms was used. Winter soil temperatures at depths of 80 cm, 120 cm, 160 cm and 240 cm were plotted, based on deep soil thermometer data and the outline of the spadefoot's range was compared with close-to-zero isotherms in deep soil. Within the range of this species, the depth of the position of zero isotherms increases eastwards: from 80 cm in European Russia, to more than 160 cm in the south-west of Western Siberia. The eastern boundary of the species' range lies in the forest-steppe, steppe and semi-desert zones in the Tobol-Ishim interfluvium and further south, on the left bank area of the Turgai River. This boundary clearly coincides with the zero isotherm, which lies here at a depth of 160 cm, forming an impermeable barrier to the spadefoot's distribution.

Key Words

cold tolerance, freezing soils, geographic range, overwintering

Introduction

The geographic range of any organism is formed as the result of a complex process influenced mainly by two components: paleogeographic events and current environmental factors. It is not an easy task to evaluate the role of these components, especially in territories with a complex paleogeographical (quaternary) history. This fully applies to the geographic ranges of amphibians.

An example of this phenomenon is the range of a common amphibian species, the Pallas' spadefoot, *Pelobates vespertinus* (Pallas, 1771) (Anura, Pelobatidae), which occupies part of European Russia, ranging to the south-

west of Western Siberia to the east and suddenly ending without any obvious physical natural reasons as to why.

The western border of the range in Europe is located approximately 36°E. This line running from the Crimean Peninsula to around 57–58°N (the northern boundary of mixed coniferous-broad-leaved forest) indicated the contact zone of the Pallas' spadefoot and the common spadefoot, *Pelobates fuscus* (Laurenti, 1768) (Litvinchuk et al. 2013; Dufresnes et al. 2019a, b). In the south, the species occupies an area up to the semi-deserts of the Caspian Depression (Bykov et al. 2009; Debelo and Chibilev 2013; Askenderov et al. 2017), where it penetrates via river valleys, agricultural ecosystems, canals and settlements.

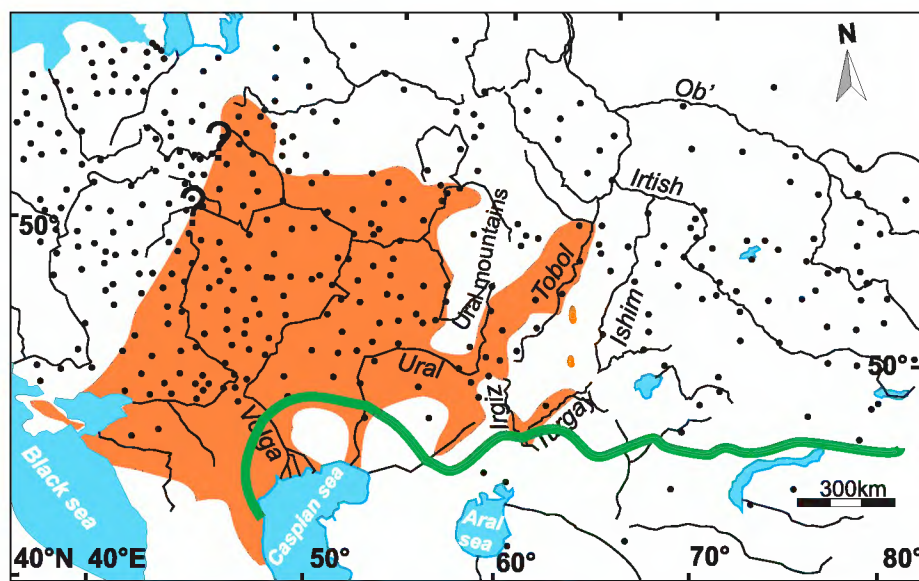


Figure 1. Range of the Pallas' spadefoot, weather stations and the boundary of the desert zone. Geographic range of the Pallas' spadefoot (shaded), weather stations with soil thermometers (black dots) and the northern boundary of the desert zone (green line).

However, eastwards of the Ural Mountains, this species has a very limited distribution in the extreme south-west of Western Siberia including some areas in north-west Kazakhstan (Fig. 1).

Here, in the Emba River's headwaters, the left tributaries of the Tobol and after the confluence of the Ubagan directly through the valley of Tobol, the spadefoot is found regularly (Dinesman 1953) and also in isolated populations: in a linear fashion – along river valleys and in a non-linear fashion, such as in the hollows of lakes. The eastern boundary of the spadefoot's range is formed by several isolated populations in the Ubagan, Irgiz and Turgai valleys and in the interfluvium of the Turgai and Ubagan (Fig. 1). The spadefoot is not found eastwards of the Turgai or in the watershed of the Ishim River. Its absence beyond the Turgai is easily explained by the aridity of this territory (National Atlas of the Republic of Kazakhstan 2010) and, as a consequence, the rarity of puddles resulting from rainfall and thawing snow. However, the interfluvium of the Tobol and Ishim Rivers lies in the steppe and partially in the forest-steppe zone. It is hard to explain the boundary of spadefoot's range in this area by a pronounced eastwards increase in warm seasonal factors (primarily climatic ones) that would adversely affect this species. Mesophytic habitats, which appear to be suitable for the spadefoot, are common near the lakes both in this interfluvium and further eastwards amongst various type of steppes and northwards of the forest-steppe ecosystems. The reasons for the absence of this species to the east of the aforementioned border are not entirely clear. Therefore, formulating a hypothesis also proves difficult, due to a lack of knowledge of the ecology of this strictly nocturnal, obligatory burrowing species (Iosif et al. 2014).

One of the most important eco-physiological characteristics of the Pallas' spadefoot is its lack of resistance to negative temperatures. The spadefoot is one of the least tolerant Boreal anuran species overwintering in soil (Berman et al. 2019). Animals collected close to the city of Saratov (within the boundaries of the range of *P. vespertinus* according to the chart of their

distribution by Dufresnes et al. 2019a) are unable to withstand negative temperatures. In the experimental group, only 20% of the individuals of *P. vespertinus* survived -1°C for 3 days in supercooled conditions (Berman et al. 2019). At the same time, other Boreal anuran species which we investigated that overwinter in soil and do not tolerate freezing temperatures, remained alive at this temperature (-1°C) (and also in supercooled conditions) for considerably longer, for example, toads *Bufo bufo* and *B. raddei*, 100% survive for at least 30 days. Moreover, even those frog species that avoid negative temperatures and overwinter in water, can tolerate a slight negative temperature better than the spadefoot. For example, in *Rana temporaria*, *R. amurensis* and *R. dybowskii*, all individuals survived at -1.5°C for 10 days (Berman et al. 2017). In other words, the spadefoot appears to be the least cold-resistant amphibian species of the temperate zone and it quickly dies when the temperature drops slightly below 0°C (Berman et al. 2019).

Therefore, a limiting factor for the spreading of *P. vespertinus* could be negative temperatures during the period of wintering, which the spadefoot spends in the soil, at a depth of between 40 cm and 1.5–2 m (Bannikov and Denisova 1956; Iskakova 1959; Debelo and Chibilev 2013; Yermokhin et al. 2013).

The goal of this work was to analyse the winter temperature regimes in the soils within the geographic range of the Pallas' spadefoot and to estimate their role in the formation of the eastern boundary of the range. The particular target was to compare the relative position of the eastern border of the spadefoot's range with close to 0°C isotherms that were revealed during the analysis.

Material and methods

To achieve our goal, we used a cartographic approach. Within the borders of the map of the distribution of the common spadefoot *Pelobates fuscus* (Kuzmin 2012), corresponding with the work of Dufresnes et al. (2019a, b), the range of the separate species, *P. vespertinus*, has recently been defined. In addition to this, a detailed list of findings of Pallas' spadefoot on the eastern border of the range has been compiled (Suppl. material 1: Table S1). On this basis, the updated outline of the Pallas' spadefoot range can be seen in Fig. 1.

Within the obtained outline and in the adjacent areas, we plotted the position of all 390 weather stations of the Federal Service for Hydrometeorology and Environmental Monitoring of Russia (Roshydromet), which measure soil temperatures at the standard depths (80 cm, 120 cm, 160 cm, 240 cm and 320 cm) (The Handbook on the Climate of the USSR 1964–1966). For each weather station, we used the average temperature of the coldest month, measured at the five above-listed depths, rather than the minimum temperatures, which are not published in the reference books. The difference in these characteristics

is insignificant: in the southern part of West Siberia, the annual minima at depths of 1.6–3.2 m differ from the average temperatures of the coldest month only by 0.3 °C or less (VNIIGMI-MCD 2019).

Overall, our constructed isotherm schemes characterise the temperature stratification in the ground within the geographic range of the Pallas' spadefoot. It is important that we used the most comprehensive databases of ground temperatures which exist today. The data from the weather stations were obtained from the 1930s to the 1960s, the most recent period of climate stability (Anisimov and Zhiltsova 2012).

Results and discussion

The spadefoot's range and ground temperatures

Naturally, the distribution of isotherms significantly differs at various soil depths. In the European part of the range, the location of the isotherms reflects the basic trend of winter temperatures falling from southwest to northeast. At a depth of 80 cm, winter temperatures are positive in most of the studied area, except for the regions eastwards from the Volga River (Fig. 2). At a depth of 120 cm, the zero isotherm lies much further to the east, already in the watershed of the Ural River and in the Trans-Ural area. Within the range of the spadefoot, although only in its eastern part, zero temperatures were recorded even at a depth of 160 cm. This isotherm forms a closed contour and encompasses the territory of the Tobol-Irtysh interfluvium and in part, the area towards the east of the Irtysh River, forming a so-called "cold core". Here, positive temperatures are recorded only at a depth of 240 cm; the closed negative isotherm seen in the previous schemes is almost completely dispersed (Fig. 2).

Comparison of the obtained isotherm scheme and the fact that spadefoot's cold tolerance is only 0 °C (Berman et al. 2019), allow us to conclude that, within the main part of the European range, this species can overwinter underground, digging to a shallow depth (less than 80 cm). As we move eastwards, this depth of wintering should increase and in west Kazakhstan, the spadefoot can avoid negative temperatures, presumably only by digging at least to 120 cm. At the eastern boundary of its range, it could overwinter only at a depth of 160 cm or more. Indeed, scholars who studied the spadefoot's ecology at the eastern boundary of the species' range report that it overwintered much deeper than it does in Europe, at 1.5–2 m (Iskakova 1959; Vershinin 2007; Debelo and Chibilev 2013).

However, the spadefoot does not penetrate in the interfluvium of the Tobol and Ishim Rivers. The reason for such geographic distribution is clearly the distribution of soil temperatures at the depth of overwintering. Our map of the 160 cm depth (Fig. 2) clearly shows that

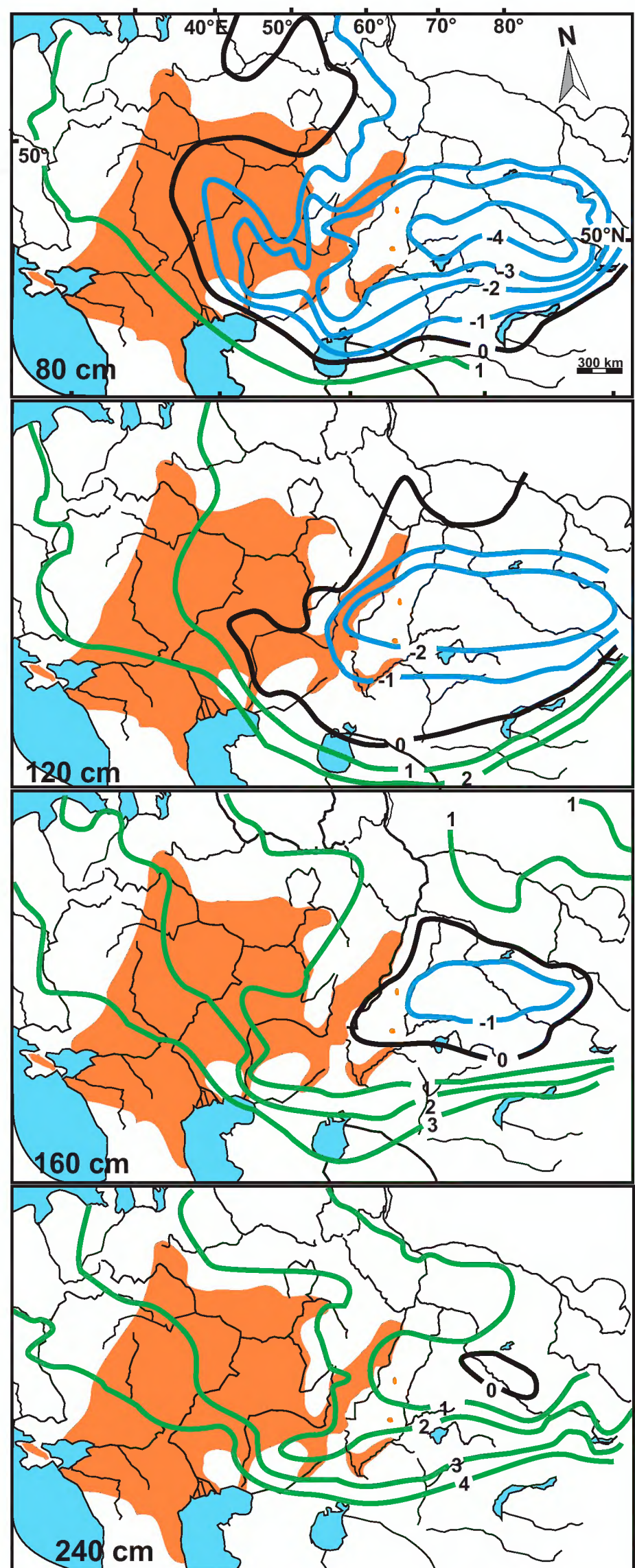


Figure 2. Soil isotherms (°C) in the coldest months and range of the Pallas' spadefoot (shaded). Soil isotherms (°C) at different depths in the coldest months: European Russia, southern West Siberia and west Kazakhstan. Geographic range of the Pallas' spadefoot (shaded), numbers in the left lower corners represent depth of the measurement made by weather stations.

eastwards from the Tobol, the outline of the zero isotherm coincides with the eastern boundary of the spadefoot's range.

Temperature conditions along the eastern boundary of spadefoot's range

This coincidence of the border of the range of the spadefoot and the location of the zero isotherm at 160 cm, is even more pronounced on an enlarged map, where the actual soil temperatures for the coldest months, rather than generalised isotherms, are plotted (Fig. 3).

A latitudinal transect from the Ural River to the upper Tobol and further to the Ishim, at a depth of 160 cm, clearly shows a gradient from slightly positive (0.6–2.4 °C) to slightly negative temperatures (-0.3– -1.6 °C). This gradient is so stable that even with only a few weather stations existing, one can see the possible position of the zero isotherm. Further north and east, the soils in the Tobol-Ishim interfluvium at a depth of 160 cm, are just as cold as those in Tobol's headwaters; this fact is confirmed by all weather stations, many of which are present east of the River Ishim.

The location of the eastern border of the range is described on the basis of literary data, dating, in the main, from 1946 to 1995 (Suppl. material 1: Table S1). The position on the zero isotherm is according to the data of the 1930s to 1960s (a period of climatic stability). However, according to the data from 14 current weather stations, (VNIIGMI-MCD 2019) close to the eastern edge of the spadefoot range, warming started in the second half of the 1970s. In the 90s, the average ground temperature, at a depth of 160 cm in the coldest month, had increased by between 0.0 and 1.6 °C. If the warming trend continues, a shift of the spadefoot range to the east may occur (Fig. 3).

The green toad *Bufotes sitibundus*, a species recently separated from the *B. viridis* complex (Dufresnes et al. 2019c) is distributed far further to the north-east than the Pallas' spadefoot, in the watersheds of the Ishim Riv-

ers and further on the same latitude, reaching the River Irtysh. The cold tolerance of *B. sitibundus* is not much higher than that of the spadefoot; according to our unpublished data, it can survive for 7 days (or possibly even more) at -1 °C, but it does not tolerate -3 °C. The difference in geographic ranges may be due to the behavioural features of these species. The spadefoot burrows by itself, while *B. sitibundus* mainly uses the burrows made by colonial rodents and penetrates underground to reach an acceptable temperature level.

Conclusions

Our study demonstrated that the eastern boundary of the spadefoot's range is determined largely by current climatic factors rather than by paleogeography. The range of this species is limited from the south-east by increasing desertification; from the east, by deep freezing of the soils (more than 160 cm); and from the northeast, probably by the same combination of zonal conditions as at the northern boundary of this species' range in Europe.

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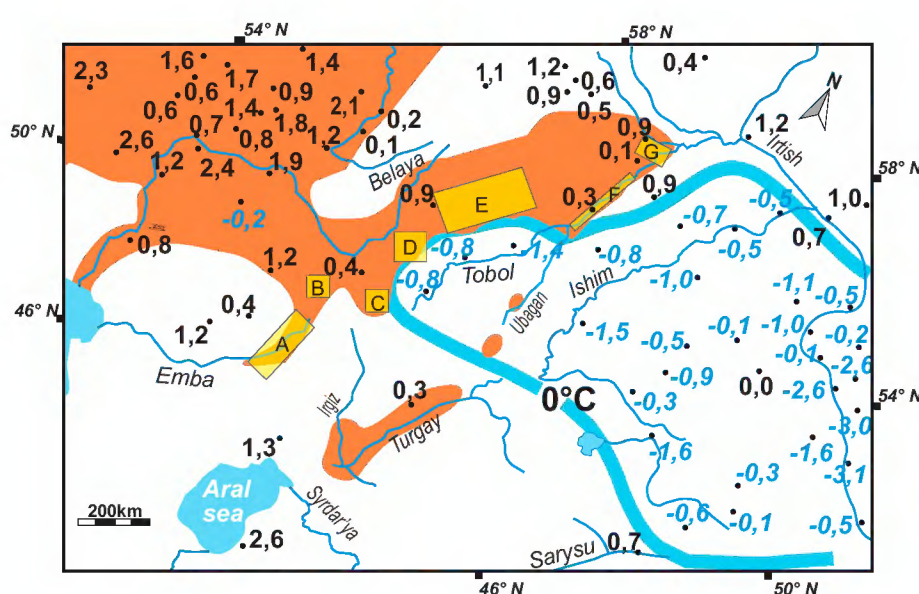


Figure 3. Soil temperatures of the coldest month to the east of range of the Pallas' spadefoot. Average soil temperatures of the coldest month at a depth of 160 cm in the eastern part of the geographic range of the Pallas' spadefoot (shaded). Numbers represent temperature (°C); wide blue line – isotherm (0 °C). Rectangles with letters – the territories with the easternmost points of spadefoot's finding (excluding enclaves). Names and coordinates of these points – in (Suppl. material 1: Table S1).

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Supplementary material 1

Table S1

Authors: Nina Bulakhova, Arcady Alfimov, Daniil Berman

Data type: occurrences

Explanation note: Location of points of spadefoot findings on the eastern boundary of range.

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